

HOMINOID EVOLUTION AND CLIMATIC CHANGE IN EUROPE

VOLUME 1

# **The Evolution of Neogene Terrestrial Ecosystems in Europe**

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# 1 Introduction

Jorge Agustí, Lorenzo Rook and Peter Andrews

The late Neogene (the period between – 14 and – 2.4 Ma) is one of the most interesting phases in understand the present configuration of terrestrial ecosystems. It was during this time that the change took place from the middle Miocene dominant subtropical forests that stretched across southern Europe and western Asia to a more open but still wooded biotope that now prevails in warm-temperate areas. This change in vegetation, which strongly affected the composition of mammalian faunas, seems to be linked to the rapid spread of grasses around 8–10 Ma ago. Moreover, in the late Neogene, climatic shifts and falling temperatures due to the spread of the Antarctic Ice, were followed by the Plio-Pleistocene Arctic glaciations in the Northern Hemisphere. Furthermore, during the late Neogene, important changes at the regional level gave rise to the present configuration of the Old World land masses, and the successive drying of inland seas in the European area facilitated faunal interchange between Europe and Central Asia and Africa. At the same time, other tectonic processes like the Himalayan and the Tibetan uplifts and the opening up of the great eastern African basins and Red Sea, although working in opposite directions, favoured the processes of speciation and isolated evolution.

All these phenomena must have had a strong influence on hominid evolution between 14 and 2 million years ago (Ma). The diversity of hominid species recorded in that period must be considered in relation to the changing environmental conditions and to constrictions imposed by the existence of significant zoogeographical barriers. As a consequence, at around 10 Ma ago Eurasia displayed a large variety of apes, with gracile forest-dwellers (*Dryopithecus*, *Sivapithecus*), dry-adapted forms (*Ankarapithecus*) and large robust gorilla-like forms (*Graecopithecus*), and all this variety in a period when there is a huge information gap in Africa. In some ways, the Eurasian Miocene radiation of apes parallels the trends observed in Africa 5 Ma later that led to the appearance of the first bipedal hominids. Differing from the Pliocene hominid evolution in Africa, the changing environments did not result in Eurasia in the emergence of bipedal apes, but in the extinction of generalised morphotypes and the persistence of highly specialised forms in relic areas (*Gigantopithecus*, *Pongo*). However, knowledge of the ecosystems in which hominids of the late Miocene evolved is still incomplete, and very little integrated analysis of data has been attempted, in particular making use of modern techniques for palaeoenvironmental analysis such as isotopes, pollen, micromammals.

In order to focus on these issues and to foster co-operation between scientists dealing with them, the scientific network 'Hominoid evolution

and environmental change on the Neogene of Europe' was approved by the European Science Foundation in 1995. One of the goals of this network was to create a database on Neogene Mammals of Eurasia, that could be used for further analysis of the ecosystems where hominoids lived. The network also organised three workshops in order to analyse different aspects of the late Neogene time and their relevance to hominoid evolution.

The first workshop was held in Sant Feliu de Guixols (Spain), from the 24th to the 27th of October 1997, and had as the main topic 'The Vallesian'. For analysing this particular interval of the late Miocene, 24 scientists from 11 countries attended this first workshop. The workshop was mainly devoted to analysing the faunal and environmental changes that took place during the period known as the Vallesian stage. However, this analysis was not strictly limited to that period but included also the intervals immediately preceding and succeeding the Vallesian (eg., late Aragonian and early Turolian). In this way, a number of presentations dealt with regional mammalian successions ranging from Spain to Southern Asia: Spain (Agustí *et al.*, Morales *et al.*), France (Mein), Italy (Rook & Engesser), Central Europe (Franzen & Storch), the Aegean area (Koufos & De Bonis), Anatolia (Fortelius *et al.*) and Eastern Europe (Nesin & Topachersky). In the case of Eastern Spain, the communications presented by the Spanish team were complemented with a field-trip in the Vallès-Penedès Basin, which enabled the participants to have an accurate idea of the work developed in this area.

The emphasis of the workshop was put on the comparison and close correlation of long sections bearing sequences of large and small mammal localities, instead of the usual correlation between isolated localities lacking an accurate geological context (for instance, in the case of karstic fissure infillings). In this way, comparison could be made between sections bearing a detailed magnetostratigraphic analysis, particularly the sections of the Potwar Plateau (Pakistan), the Vallès-Penedès (Spain) and Sinap (Turkey). Another significant topic of the workshop was the so-called 'Mid-Vallesian Crisis', an extinction event that followed the change from the middle to the late Miocene. Results reviewed at the workshop suggested that a change similar to the Mid-Vallesian Crisis of Western Europe occurred at different times in different areas. The change was already established in the early Vallesian in the so-called Sub-Parathetian Province (data from Maragheh by Bernor), but in Western Europe did not take place until about 9.6 Ma ago (data from the Vallès-Penedès by Agustí and co-workers). On the other hand, in Central Europe, several species indicating wet, forested conditions persisted well into the late Vallesian (data from Franzen & Storch). Finally,

such a change was not seen in Southern Asia (Pakistan) until 8–7.2 Ma (data from the Potwar Plateau).

The second workshop took place in Certosa di Portignano (Siena, Italy), devoted to the ‘Climatic and environmental change in the Neogene of Europe’; 25 scientists from 11 countries and different palaeoenvironmental disciplines had the rare opportunity to experience a real interfacing of data from the terrestrial ecosystems, the shallow marine realm and the deep sea. A first set of contributions dealt with the palaeogeographic evolution of the Tethys area and the effects of changes in the extent of the Tethys sea on faunal distributions and climate evolution. F. Rögl (Vienna) presented a sketch of the evolution of this area from the early Tertiary to the late Miocene. With the contact between the Arabian plate and the Anatolian plate, land bridges formed between Africa and Eurasia opened and closed throughout the middle Miocene, beginning about 19 Ma. No hominoid primates are known this early in Europe, but of particular significance to hominoid migrations was the end-Burdigalian regression of the sea at around 16 Ma, as this coincides with the earliest evidence of hominoids in central Europe.

Contributions to climate modelling during the late Neogene were provided by P. B. DeMenocal & F. H. Brown, and by E. O’Brien. According to DeMenocal & Brown, marine records of African climatic variability document a shift toward prolonged and seasonally more arid conditions after 2.8 Ma. This is linked to cold North Atlantic sea-surface temperatures associated with onset of Arctic Ice sheets. Major changes in African faunas coincide with this climatic change suggesting that some speciation events may have been climatically mediated. E. O’Brien demonstrated that a large proportion (79%) of African woody plant species richness is accounted for by two aspects of climate, annual rainfall and an optimised function of energy (minimum monthly potential evapotranspiration). Finally, the palaeobotanical approach included the point of view of the palynological analysis (J. P. Suc, A. Bertini, G. Clauzon & D. Subalyova).

Evidence for climate change was considered both from invertebrate and vertebrate evidence. Data presented by Rosen demonstrated that most coral reefs (and their associated *z*-corals) occur in the Mediterranean area in three major high sea-level phases, corresponding to the early (Aquitania), middle (Langhian–Serravalian) and late Miocene (Tortonian–early Messinian). Small mammals were discussed by Reumer (Insectivores), Daams *et al.* (rodents from Central Spain) and Agustí *et al.* (mainly rodents from Eastern Spain). According to Reumer, ecological studies have shown that environmental moisture may be the ultimate determinant of within-habitat diversity and numerical abundance of soricids, which can be taken as a good



indicator of relatively warm and humid palaeoclimate. Shrews (Soricidae, Insectivora) are among the most relatively sensitive mammals against climatic shifts because of their small size and high surface/volume ratio. Three main periods of faunal turnover, corresponding to humid and warm conditions, characterise the Neogene history of shrews: the early Miocene (19–20 Ma), the early–late Miocene (Vallesian; 9–11 Ma), and the latest Miocene to Pliocene (6 and 2.5 Ma). Climatic deterioration at around 2.7–2.3 Ma finally caused a severe reduction of the European shrew fauna. Among rodents, the analysis of the Calatayud-Daroca succession developed by Daams and co-workers also suggests, as for the shrews, that species diversity is more related to relative humidity than to temperature. Quantitative analysis of the rodent succession developed by Agustí and coworkers in the Vallès-Penedès Basin allows the recognition of an alternation of dry and humid phases during the Miocene and early Pliocene times. Early Miocene localities indicate forested, humid conditions, similar to those recorded in the early Miocene of Central Europe. Increasingly dry conditions are recorded across the late early and middle Miocene (early middle Aragonian), but a return to more humid conditions is observed in the late Aragonian (Serravallian) times. The middle/late Miocene boundary coincides with a relatively dry period, followed again by a humid peak in the early Vallesian (early Tortonian), and it is this time that coincides with the maximum abundance of hominoid remains in Western Europe. Again, as in the case of shrews, it appears that species diversity is more related to relative humidity than to temperature.

Contributions dealing with large mammal associations were those of N. Solounias, M. Plavcan, L. Witmer & J. Quade, L. de Bonis & G. Koufos, L. Kordos, and R. Bernor. After a detailed analysis based on a variety of sources (dental and postcranial ecomorphology of bovids, palynology, isotopes), Solounias and co-workers arrived to the conclusion that the main habitat of the Pikermian mammals was not a savanna ('the savanna myth'), but sclerophyllous evergreen woodland similar to today's mixed monsoon forest and grassland glades of north Central India. Large mammals with lucky exaptations migrated into Africa from the Pikermian bioprovince. A similar topic was developed by de Bonis & Koufos, who found in Greek faunas evidence of a trend towards drier conditions in the late Miocene. On the other hand, the disappearance of hominoids and other forest elements in the Pannonian Basin at 9–7 Ma was attributed by Kordos to the regression of the Pannonian sea rather than to a general climatic trend. Finally, Bernor & Andrews discussed the patterns of hominoid immigration, dispersal and extinction. Hominids entered Europe in the middle Miocene because land crossings of the Tethys were possible at this time and the subtropical forest

environments were suitable. By virtue of the taxonomic diversity and restricted biogeographic ranges alone, Eurasian Miocene hominids show strongly vicariant evolutionary patterns. This suggests a model whereby a founding species extends its range under favourable and specific environmental circumstances and then becomes geographically restricted to refugia by geographic (= tectonic and palaeogeographic) and/or environmental events. A frequent byproduct of vicariance, exercised over millions of years time, is homoplasy, and it is evident that there was a great deal of homoplasy in Miocene hominids.

The nature of the environments occupied by apes in Europe had many structural similarities with the environments in Africa with which they are associated at this time. Palaeoecological evidence suggests that African middle Miocene apes lived in seasonal woodlands and forests, for example at Fort Ternan and Maboko Island. The hominids at these sites were partly terrestrial and with their large thick-enamelled teeth were adapted for similar diets to some of the European apes. The earliest European apes were similar in being both partly terrestrial and with almost identical dietary adaptations. The community structure of the mammalian faunas in the African and European sites were extremely similar, and by inference the ecosystem they occupied was also similar. The similarities in locomotor and dietary adaptations of the African and European apes at this early stage indicate further that their position in their respective ecosystems was also very similar. In one sense, therefore, these middle Miocene taxa in Europe were not as distinct from their African relatives as taxonomic divisions and their geographic separation may appear to indicate.

Towards the end of the middle Miocene, at 13–12 Ma, the trends of partial terrestriality and thick-enamelled frugivory continued in a group of fossil apes assigned either to the pongine clade or to a paraphyletic group unrelated to any living. They are associated with a range of open forest to woodland environments ranging from southeast Europe to China, and one genus at least may be related to the orang utan. At the same time, the more arboreal and suspensory *Dryopithecus* emerged in association with closed subtropical forest environments where they are sometimes found associated with *Pliopithecus* and *Anapithecus*. Similar environments and a similar, possibly heritage, adaptation for suspensory locomotion persisted in *Oreopithecus*, although it has recently been argued that this fossil ape may also have had adaptations for terrestrial bipedal mode of locomotion and the evolutionary relationships of *Oreopithecus* are still unclear.

Later in the Miocene, the Alpine–Himalayan orogeny caused major changes in land–sea relations, global climatic circulation patterns and seasonality particularly in Central Asia. Regression of the Paratethys likewise

- 6 caused a shift of habitats to greater seasonality and replacement of ever-green subtropical forests by deciduous woodlands and, progressively in the late Miocene, more seasonal warm temperate woodlands with progressively more open habitats. Hominid primate distribution tracked these changes closely during the 12–9 Ma interval, contracting their range from both west and east and finding temporary refuge in southeastern Europe, where favourable subtropical conditions persisted for a time after being lost elsewhere. Hominids disappeared from this region finally during MN11, although they persisted until MN12 in local insular habitats in Italy and the latest Miocene of China.